The importance of globalisation in driving the introduction and establishment of alien species in Europe

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ABSTRACT

Understanding the role of globalisation in promoting introduction and establishment of alien species is an important step towards successful management of biological invasions. We aimed to quantify the taxon-dependent association of globalisation with the introduction and establishment of alien species in Europe. The availability of the KOF Index of Globalisation that measures all economic, social and political dimensions of global connectivity enables a study of this factor. Based on an extensive database of alien species, we used model selections based on the Akaike Information Criterion and hierarchical partitioning to identify the importance of globalisation in predicting the number of all introduced species and established species of ten mainly terrestrial taxa in countries across Europe. The association of globalisation with alien species establishment varied depending on taxon type. While the gross domestic product (GDP) of countries was a strong predictor for all but one taxon, globalisation was also found to be an important predictor for three taxa including those of high (e.g. insects) and low mobility (e.g. magnoliophyta). Globalisation explained 3.1 to 22 % independently, and 5.5 to 35 % jointly with other variables, of among-country variations in the number of established alien species. The effect of globalisation on the distribution of all introduced species is not substantially different from that on the established alien species. This study highlights how globalisation among habitat availability and environmental conditions can determine the patterns of alien species introduction and

establishment across Europe. The results also emphasise the varying degree of importance between different taxa. Knowledge of the relative significance of various pathways with regard to different taxa is important for correctly focusing efforts to reduce the spread of these species.

INTRODUCTION

Humans have traded and transported plant and animal species for thousands of years, but with the modernisation of trade, technology and travel and the resulting globalisation of the world, there has been a substantial increase in the rate of spread of alien species (Hulme 2009). Alien species are defined as taxa occurring outside their natural range due to direct or indirect introduction by humans; invasive alien species are a subset of these, named as such if they become established and threaten native biodiversity and both economic and social resources (IUCN 2000). Invasive alien species are widely regarded as playing a significant role in anthropogenic global environmental change (Vitousek et al. 1997) and causing substantial negative effects both from ecological and economic perspectives. Invasive species are, for example, second only to habitat destruction as a threat to biodiversity in the U.S. (Wilcove et al. 1998). Furthermore, the annual monetary impact of invasive species in Europe is estimated to be approximately €10 billion (European Commission 2008), and even this figure is an underestimate as the potential ecological and economic impacts are only known for about 10% of European invasive species (Vilà et al. 2010). Alien species are thus a problem of growing importance and attention.

The different ways by which alien species are introduced to a location are increasingly being recognised as playing an important role in determining the likelihood of establishment, and thus are of great importance in predicting future trends in the spread of alien species. Many studies have named globalisation – defined as the process by which the world is becoming increasingly interconnected through the global network of trade, communication, immigration and transportation (Financial Times; http://lexicon.ft.com/) – as a key driver of the increasing number of alien species (Lockwood et al. 2005; Perrings et al. 2005; Lodge et al. 2006).

Several factors such as income growth and transport efficiency (Hulme 2009) or shipping activity (Jackson & Grey 2013) have frequently been used as proxies of globalisation. However, such specific proxies may not fully quantify the effects of globalisation. Whilst trade is widely used to analyse the effects of globalisation (e.g. Levine & D'Antonio 2003), other aspects of globalisation such as travel may also play a vital role in determining the spread of alien species. For example, a study in the United States found that at least 449,500 pest interceptions at ports of entry or border crossings (from 1984 to 2000) were associated with international travel (McCullough et al. 2006). Another study found that tourists have accidentally introduced non-native seeds to pristine areas (Chown et al. 2012). These findings thus highlight the significant importance of aspects of globalisation other than solely trade.

This study focuses on Europe, where the rate of introductions of alien species is increasing each year (DAISIE 2009), consistent with exponential increases in trade and transport (Hulme 2009). The KOF Index of Globalisation (Dreher 2006; http://globalization.kof.ethz.ch/) – which measures the global connectivity, integration and interdependence in terms of economic flows, information accessibility, social contact and cultural proximity (i.e. does not accounts solely for trade and travel activities) – provides an excellent opportunity to analyse globalisation in relation to the number of alien species. Such an integrated measure of globalisation may not well reflect each of the different invasion processes, but is expected to represent the propagule pressure associated with globalisation that each country faces. Additionally, the recently updated DAISIE European Alien Species Gateway (DAISIE; http://www.europe-aliens.org/) database allows for an analysis at a continental scale across a wide range of taxa. This database, which is freely available online, aims to produce an inventory of all alien species, across all taxonomic groups and in all European countries (where information is available). Furthermore, it does not only rely on data from published case studies, but also includes, for example, records from various collaborators and checklists (for more information, see DAISIE 2009). Thus the effect of publication bias should be minimal in this database. But inherently, such database is subject to sampling bias such as sampling inconsistencies between countries and data misclassification (Lambdon et al. 2008).

The availability of a worldwide globalisation index and a European database of alien species offer new approaches to the study of the importance and impact of globalisation on the distribution of alien species. This paper, therefore, aims to analyse the relationship between globalisation and establishment of alien species across Europe in a variety of taxa. This paper also explores the effect of globalisation on introduction of alien species (i.e. including non-established alien species) to determine if globalisation is of the same importance for these two steps of biological invasion process.

METHODS

Data collection

This paper used the data collected from DAISIE for 65 European countries, administrative regions or major islands (referred to as "regions" throughout this paper) with respect to the number of alien species per taxa in each of 4 groups: established (species that has formed self-reproducing population), not established (the occurrence is considered causal or incident; i.e. a species has not formed self-reproducing population), extinct (once established and now extinct) and unknown. This paper focused on two datasets – all introduced species (i.e. including all established, non-established and extinct species) and only established species – to investigate the importance of globalisation in introduction and establishment, the two steps of the process of biological invasion. The taxonomic groups investigated in this study, which include very different taxonomic level from class (e.g. mammal, bird) to realm (e.g. fungi), followed those used in DAISE. Therefore this study investigates the effect of globalisation on (1) the number of all introduced species per region and (2) the number of established alien species per region, for each taxonomic group.

We used the KOF Index of Globalisation of the year 2013 (Dreher 2006) for this study. This state-of-the-art index of globalisation encompasses all three main dimensions of globalisation, namely economics, social and political. The economic aspect includes information on actual economic flows and restrictions on trade and capital. Social globalisation comprises data on personal contact between countries, information flows of ideas and images, and cultural proximity. Finally, political globalisation is defined by the diffusion of government policies. The KOF globalisation index was calculated on a yearly basis where each of the variables above was transformed to an index on a scale of one to one hundred. The economic, social and political aspects each carry a different weight (i.e. 36%, 37% and 26% respectively) that was determined with the principal components analysis for the entire sample of countries and years (for details see http://globalization.kof.ethz.ch/media/filer_public/2015/03/04/method_2015.pdf). The overall globalisation index is on a scale of 1 to 100, with higher values denoting greater globalisation.

Biological invasions of alien species have occurred over several centuries (Lambdon et al. 2008), and thus there are potential problems with using an index that describes current globalisation with no inclusion of possible historical trends. Such a problem has been highlighted previously with respect to the use of, for example, GDP or trade flows; both are current economic indicators and thus not properly representative of historical patterns (Pyšek et al. 2010), which are likely to have influenced the spread and current distribution of alien species. A previous study (Essl et al. 2011a) has also highlighted this "invasion debt", whereby current patterns of alien species richness more closely reflect historical socioeconomic factors, particularly for more mobile taxa such as insects and birds. Admittedly, many species recorded in the DAISIE database were originally established a long time ago (1900s). Historical globalisation metrics (though unavailable), therefore, may be a better predictor of current distribution of introduced or established alien species. However, since the export GDP – a rough proxy of globalisation – of 28 European countries in 1900 and 2000 are highly correlated (Spearman coefficient = 0.87, P <0.001; data from Essl et al. 2011a), we argue that the 2013 KOF globalisation index has high relevance to the historical globalisation levels as well. Therefore, the current globalisation level of a given country should also reflect its historical level of international socio-economic activity.

Besides globalisation index, we included 10 other explanatory – potentially confounding – variables for each region in this study to account for factors already known to affect alien species richness: (i) area (Central Intelligence Agency 2013); (ii) GDP (Central Intelligence Agency 2013); (iii) mean annual precipitation (Mitchell et al. 2003); (iv) mean annual temperature (Mitchell et al. 2003); (v) continentality (expressed as difference in mean January and July temperature; Mitchell et al. 2003); (vi) population density (calculated from population size and area; Central Intelligence Agency 2013); (vii) road density (World Bank Group 2014); (viii) percentage of agricultural land (World Bank Group 2014); (ix) percentage of forest (World Bank Group 2014); and (x) insularity (island versus continent; yes/no). Area was included to account for species-area relationships (McKinney 2006). GDP has also been shown to correlate significantly with the number of alien species (Hulme 2009). Continentality, mean annual precipitation and mean annual temperature were included in order to account for the effects of climatic factors, which have previously been found to affect alien species richness (e.g., Shi et al. 2010). Continentality was expected to be negatively correlated with alien species richness, with a more stable year-round temperature likely allowing alien species a better chance of finding the climate suitable. Human population density has been shown to be positively correlated with alien species richness (Pyšek et al. 2010), and road density is likely also to aid dispersal (Hulme et al. 2006), increasing the number of alien species. Percentage agricultural land and forest were also expected to be correlated positively with alien species richness (Ehrlich 1989). Finally, islands are more highly invaded than mainland regions (Lonsdale 1999). Admittedly, some of these explanatory variables may not be biologically important in all taxonomic groups, but we decided to use the same set of explanatory variables in all taxa for consistency. Any unimportant variables would simply be excluded in the most parsimonious models selected by AICc or show a low explanatory capacity in a hierarchical partitioning within each taxonomic group (see **Statistical analysis** below).

Statistical analysis

Pearson product-moment correlation coefficients were first used to determine any possible correlations between explanatory variables. When the coefficient between a pair of variables was greater than 0.8 or less than -0.8, we omitted one of the variables from the following analysis. This applied to road density and population density and road density and area, with road density subsequently excluded from the analysis (Table A1).

For both all introduced species and established species datasets, only taxonomic groups with species in more than 25 regions were retained for this study (so that we could have at least 25 data points for each group), considering that we used ten explanatory variables in the analysis. Therefore, only ten taxonomic groups in the datasets were retained. These taxonomic groups included mammals (number of regions for which data were available, n = 52 for both established and introduced species; the highest number of established species in a region, S_E = 17 species; the highest number of introduced species in a region, S_I = 39), birds (n = 47 [established] and 48 [introduced] regions; S_E = 18; S_I = 56), fungi (n = 48 regions; S_E = 56; S_I = 58), terrestrial chromista (all algae including the colourless related forms; n = 43 regions for both established and introduced species; S_E = 7; S_I = 7), terrestrial magnoliophyta (all flowering plants; n = 39 [established] and 42 [introduced] regions; S_E = 1,266; S_I = 2,011), gymnosperms (seed-producing plants that include conifers, cycads, gingko and gnetales; n = 29 [established] and 31 [introduced] regions; S_E = 38; S_I = 50), araneae and acari (henceforth referred to as "araneae" which includes spiders, mites and ticks; n = 40 regions; S_E = 31; S_I = 31), terrestrial nematodes (n = 47 regions for both established and introduced species; S_E = 19; S_I = 19), terrestrial insects (n = 58 regions for both established and introduced species; S_E = 598; S_I = 599) and myriapods (n = 40 regions for both established and introduced species; S_E = 10; S_I = 10). Model selections based on the Akaike Information Criterion with a correction for small sample size (AICc) were then carried out for each taxon of the two datasets using simple linear regressions with the log-transformed number of species per region as the response variable, and the ten variables listed above (excluding road density) as explanatory variables. Both area and GDP were log-transformed to account for the variation across multiple orders of magnitude. We first generated a candidate set of models with all possible parameter subsets, which were then fitted to the data and ranked by Δ_i values (the difference between each model's AICc and $AICc_{min}$, that of the "best" model). Model selections were conducted using the package MuMIn (Bartoń 2012) in R (R Development Core Team 2013). A hierarchical partitioning (Mac Nally 1996) was also performed to estimate the independent and joint explanatory capacities of each of the explanatory variables separately, using the package hier.part (Walsh and Mac Nally 2013) in R. The process of a hierarchical partitioning involves computation of the increase in the fit (measured in our case as R^2) of all models with a particular variable compared with the equivalent model without that variable (Mac Nally 1996). As a result, a hierarchical partitioning provides, for each explanatory variable separately, an estimate of the independent and conjoint contribution with all other variables. As the function hier.part is known to produce a minor rounding error for analyses with more than nine explanatory variables (which is our case), we ran the analysis at least twice with the explanatory variables entered in a different order, as recommended by Walsh and Mac Nally (2013), and confirmed that the results remained the same.

Moran's I was calculated for the residuals from the full models, using the package ncf (Bjørnstad 2005) in R, to investigate the effect of spatial autocorrelation. The calculated Moran's I was between -0.37 and 0.25 up to the first 3000 km in all taxa, indicating no more than a weak autocorrelation. Thus, spatial autocorrelation was not considered explicitly in the model for the analysis.

RESULTS

For three (magnoliophyta, insects and nematodes) out of ten taxa, there was only one model with Δ_i less than 2.0, which provides substantial evidence that these are the best models (Burnham and Anderson 2002), and globalisation index was included in those models (Table 1A, B and C). The full models for these three taxa had adjusted R^2 values greater than 0.4, with that for insects greater than 0.7 (Table 1A, B and C). A hierarchical partitioning revealed that globalisation explained 3.1 to 22 % independently, and 5.5 to 35 % jointly with other variables, of among-country variations in the number of established alien species (Figure 1). Globalisation showed high explanatory capacity for the three taxa (magnoliophyta, insects and nematodes, Figure 1). The numbers of established alien species in the three taxa were positively associated with globalisation index (Figure 2). For the remaining seven taxa, globalisation index did not appear in many models with Δ_i less than 2.0 (Table 1) and also had relatively low independent contribution in explaining variations in the number of established alien species (Figure 1).

Various combinations of factors were important for each taxon, with the models of $\Delta_i = 0$ consisting of between one and four explanatory variables (Table 1). As expected, GDP was included in most models with Δ_i less than 2.0 for all but one taxon (Table 1) and also showed a high explanatory capacity (independent contribution: 2.0-23%, joint contribution: 5.8-55%, Figure 1), indicating its cross-taxa importance. Population density and percentage of agricultural land were found to be important for established alien birds and araneae, respectively (Figure 1) and positively associated with the number of established alien species (Table 1D and I). Insularity seemed to be important in explaining the number of established alien fungi, which was lower in islands, based both on model selection and hierarchical partitioning (Table 1F and Figure 1). Climatic factors were also included in top models for a few taxa; annual temperature was positively correlated with the number of established alien species for insects, nematodes and araneae (Table 1B, C and I) but negatively with myriapods and gymnosperms (Table 1G and J), annual precipitation for established alien fungi (Table 1F), and continentality for established alien nematodes, birds, myriapod, mammals and gymnosperms (Table 1C, D, G, H and J). But these climatic factors generally showed low explanatory capacities in terms of R^2 values (Figure 1).

Results were essentially the same even when using the number of all introduced alien species as the response variable, apart from the much weaker effect of population density on introduced alien birds (the result of hierarchical partitioning shown in Figure A1).

DISCUSSION

The effect of international trade on the distribution of established alien species is a subject that is often examined – using the share of exports in GDP (e.g. Essl et al. 2011a) or wealth (which also captures past levels of socio-economic activity; Pyšek et al. 2010) as proxies – and highlighted with other standard predictors. Annual socio-economic measures (e.g. GDP per capital and imports) are found to correlate with rates of introduction whereas cumulative measures (e.g. wealth) could have positive influence on the establishment of an introduced species (Essl et al. 2011a). However, it is incorrect to equate international trade or economic activities that generate wealth with globalisation. Globalisation is a broad concept covering the interdependence of countries through increasing integration of not only economic, but also political, social and legal institutions (Soubbotina and Sheram 2000). While we agree that cross-border investment flows is one of the important elements of globalisation, socio-economic measures such as wealth and the share of exports in GDP are only part of the story. In fact, the result of our analysis using both globalisation index and GDP showed that at least in three taxa, the integrated measure of globalisation was a strong predictor of biological invasion, independently from the effect of countries' wealth.

Globalisation, therefore, must be viewed as a process of political, social, legal and economic integration among countries. The globalisation index used in this study includes aspects such as international trade and travel, both of which have previously been shown to play a major role in enabling the accidental introduction of alien species. This study demonstrates that the measure of globalisation as a whole – rather than proxies for this factor – is significantly correlated with alien species richness for several taxa. Globalisation therefore is clearly important in facilitating the movement of certain taxa such as flowering plants, insects and nematodes across the world and introducing them outside their native ranges, with trade and travel increasing propagule pressure and thus the likelihood of successful establishments (Chown et al. 2012; Hughes and Convey 2010; Hulme 2009).

Contrary to many previous studies (e.g. Kobelt and Nentwig 2008; Hulme 2009), we found that globalisation has only a limited effect on the introduction and establishment of a number of the taxa. GDP was consistently the strongest predictor, independent of the effect of globalisation, for all taxa (except gymnosperm; Table 1). This implies that both economic factors and globalisation may not share a common pattern in the pathways of introduction and establishment of alien species. Broadly, deliberate release (e.g. for biological control, food, fauna 'improvement', research, etc.) and escape from captivity (e.g. from zoos, farms and pet trade) are the main introduction pathways of a wide range of terrestrial and aquatic alien taxa in Europe (Hulme et al. 2008); which are likely to be associated with economic growth and may be the mechanisms for the taxa where a relation between richness and GDP has been found. On the other hand, contaminant and stowaway are the main routes that facilitate movement for alien vascular plants in Europe (Hulme et al. 2008), a taxon where we found globalisation to be important.

In this study, we also found that climatic (temperature, precipitation and continentality) and anthropogenic (population density and agricultural land) factors were of importance for some taxa where globalisation did not play an important role in explaining variations (Table 1). Continentality seemed to be an important variable for four groups (bird, myriapod, mammal and gymnosperm), temperature for three (myriapod, araneae and gymnosperm), with population density, insularity and agricultural land important for bird, fungi and araneae, respectively. The availability of certain habitats (Chytrý et al. 2008) and the importance of climate matching between native and non-native range in determining the successful invasion of alien species has been demonstrated across a wide range of taxa, including alien fungi (Philibert et al. 2011); birds, mammals and plants (Hayes and Barry 2008); and is likely also important for spiders (araneae; Kobelt and Nentwig 2008). Hence, it is possible that these groups are more strongly limited by the environmental factors than by globalisation.

It is noticeable, for example, that there is a general decrease in the number of alien gymnosperm species at lower latitudes (Figure A2j). A negative coefficient for temperature in the model (Table 1J) selection suggests that there are greater numbers of alien gymnosperm species in countries with cooler annual temperatures. This likely reflects the climatic environment of their native range. It is thus possible that this climate preference acts as a limiting factor in the successful invasion of this group (Essl et al. 2011b), irrespective of globalisation.

The significance of environmental factors shown in the taxa where globalisation is an important predictor (e.g. insect and nematode) is consistent with the idea that globalisation increases the number of introductions and thus propagule pressure, but species also experience a strong filter for climate suitability. Thus, our ability to manage alien species will require an understanding of the synergistic effect of multiple factors.

When determining the role of globalisation in biological invasion, it is also important to consider the reasons alien species may be imported. For example, conifers are widely used in forestry in Europe, and whilst alien conifer plantations play little role in determining the subsequent gymnosperm distribution for most European countries, this is not true of countries in north-west Europe with few native conifer species (such as the United Kingdom; Essl et al. 2011b). Countries with relatively few native species are more likely to have imported alien gymnosperms in order to cultivate plantations, potentially masking any impact of globalisation.

Finally, it is possible that birds show less reliance on globalisation for their spread. Hulme et al. (2008) showed that the two primary pathways for bird introduction are intentional releases (for food/game or fauna 'improvement') and escape from managed environments (as pet or from zoos). The predominant effect of human population density on alien bird species, found in this study, may thus show the importance of attempts to improve local fauna through intentional releases as well as escape of captive species in urban cities. The establishment of some species, such as Canada goose (*Branta canadensis*), is also facilitated through adaptation to urban environments (Austin 2002), which seems to be reflected in the importance of human population density on established, but not introduced, bird species in this study. Considering their high movement capacity through flight, it is also possible that birds, once introduced and established in a certain region, have spread naturally to other regions, as believed in some species such as Canada goose, ruddy duck (*Oxyura jamaicensis*) and ring-necked parakeet (*Psittacula krameri*) listed on the European Alien Species Database (www.europe-aliens.org).

Limitations

Our analysis clearly has several inevitable limitations. First, we were not able to test the effects of interaction and quadratic terms of explanatory variables, mainly because of the small sample size relative to the number of explanatory variables considered. As a consequence, for instance, our models may not necessarily capture complex climatic conditions including variations within countries that enhance biological invasion in each taxon. Models for some taxa, such as chromista and myriapods, did not show high R^2 values, also suggesting that we could not find strong predictors of their distribution. Climatic niche can vary greatly even among similar species, and thus its effect on biological invasion needs to be explored at the species level.

Second, whilst the European Alien Species Database aims to be unaffected by sampling intensity, this has not been completely possible for all taxa, particularly the invertebrates. Sampling effort and taxonomist location likely explain the large differences between countries with respect to the number of records for established insect species, even though these are the most intensively studied of the invertebrates (Roques et al. 2009) – and thus is likely more considerable for other invertebrate taxa. Sampling bias is likely to be more significant for the less conspicuous, smaller body-size groups or those that are more difficult to identify, compared with, for example, the more conspicuous and well-studied bird and mammal classes (DAISIE 2009). However, globalisation was found to be important even for conspicuous taxa such as magnoliophyta, suggesting that the conclusions of this study are likely not affected by sampling bias.

It is also noticeable that the United Kingdom has the greatest richness for five of the 10 taxa, and is within the top 10 regions for the remaining five although there are 12 regions with land area larger than the United Kingdom (also see Figure A2). This far greater alien species richness is likely influenced by a combination of factors such as high GDP, high level of globalisation, the island status and the high population density of the United Kingdom. However, it is also possible that this large number of species is a result of the United Kingdom’s long tradition of monitoring biodiversity, and the more complete records the country has compared with many other European countries. Whilst the DAISIE project has tried to account for differences in sampling effort, it seems plausible that such bias could still occur.

In addition to this, the European Alien Species Database lists species under one of four categories: established; not established; extinct and unknown. The database lists large numbers of species as “unknown” which could potentially belong to any of the other three categories. It would seem likely that both the number of unknown species and the proportion which are actually established vary with sampling intensity. Some countries list all species within certain groups as unknown; for example all 25 alien araneae in Switzerland are listed as unknown, as are all 791 alien magnoliophyta in Ukraine. This highlights the need for further research to resolve the status of the “unknown” species.

Conclusion

This study showed that the KOF index of globalisation was a strong predictor of alien species distributions, independently from the effect of countries’ wealth. However, it was not a significant predictor for some taxa. Better understanding of the effects of globalisation with respect to specific taxa and invasive processes are crucial in order to properly inform policy and enable more effective control measures to be implemented. As a consequence of the potential delay in its effect, globalisation could be a valuable parameter for predicting the future spread of certain alien species.

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Table 1. Linear regression models investigating correlates of established alien species distribution in Europe for each of ten taxa. Each value indicates the estimated coefficient. Models are ranked according to the Akaike Information Criterion corrected for small sample sizes (AICc). Δ_i gives AICc differences between that model and the model with the smallest AICc. The models with $\Delta_i < 2$ plus one model are shown. Blank spaces show variables that were not included in the particular model.

A. Magnoliophyta. Adjusted R^2 of full model = 0.445.

Intercept	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature	AICc	Δ_i
-7.747	0.062				0.309						70.039	0
-8.276	0.060		0.281		0.335						72.391	2.352

B. Insect. Adjusted R^2 of full model = 0.702.

Intercept	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature	AICc	Δ_i
-5.927	0.018				0.347					0.057	51.206	0
-5.956	0.017				0.351			0.000		0.050	53.263	2.057

C. Nematode. Adjusted R^2 of full model = 0.517.

Intercept	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature	AICc	Δ_i
-7.559	0.025	0.040			0.232					0.068	49.483	0.000
-6.238	0.014				0.250					0.047	51.812	2.329

D. Bird. Adjusted R^2 of full model = 0.559.

Intercept	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature	AICc	Δ_i
-6.552		-0.047			0.346						58.445	0.000
-6.179		-0.035			0.317			0.001			59.286	0.841
-6.675		-0.053			0.365	-0.006					59.513	1.068
-6.257		-0.039			0.333	-0.007		0.002			59.631	1.185
-6.039		-0.058			0.348				0.000		59.843	1.398
-10.613			0.630	-0.229	0.579	-0.008					59.846	1.401
-9.809			0.520	-0.190	0.518						60.111	1.665
-1.902		-0.075		0.334			0.014	0.005			60.283	1.838
-6.065		-0.067			0.371	-0.007			-0.001		60.317	1.872
-7.509			0.437		0.335			0.002			60.426	1.981
-7.199		-0.042	0.237		0.366						60.467	2.022

E. Chromista. Adjusted R^2 of full model = 0.237.

Intercept	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature	AICc	Δ_i
-3.556					0.165				0.000		38.413	0.000
-3.418					0.173						38.646	0.234
-2.979		-0.015			0.168						39.678	1.265
-3.899					0.174				0.000	0.016	40.044	1.632
-3.784					0.182					0.016	40.065	1.652
-3.924				-0.060	0.219						40.078	1.665
-3.568					0.159	0.004			0.000		40.127	1.714
-3.371	0.007				0.150						40.343	1.931
-3.426					0.168	0.003					40.429	2.016

F. Fungi. Adjusted R^2 of full model = 0.623.

Intercept	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature	AICc	Δ_i
-6.430			-0.647		0.330				0.001		63.569	0.000
-6.142			-0.748		0.307	0.007			0.001		64.048	0.479
-8.040					0.338	0.015	0.020		0.001		64.273	0.703
-6.959			-0.485		0.311	0.013	0.012		0.001		64.876	1.307
-6.917	0.017		-0.563		0.253	0.016	0.015		0.001		65.173	1.604
-5.966	0.013		-0.856		0.261	0.009			0.001		65.354	1.785
-8.152	0.014				0.293	0.018	0.023		0.001		65.392	1.823
-6.338	0.010		-0.713		0.299				0.001		65.561	1.992
-6.326			-0.636		0.350						65.741	2.172

G. Myriapod. Adjusted R^2 of full model = 0.337.

Intercept	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature	AICc	Δ_i
-2.191		-0.035			0.161					-0.049	40.771	0.000
-4.929			0.342	-0.143	0.303					-0.055	42.070	1.299
-2.350		-0.034			0.166			0.000		-0.057	42.188	1.417
-2.893		-0.027		-0.083	0.222					-0.058	42.269	1.499
-4.018				-0.139	0.267					-0.051	42.619	1.848
-2.797		-0.030	0.178		0.179					-0.048	42.869	2.098

H. Mammal. Adjusted R^2 of full model = 0.605.

Intercept	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature	AICc	Δ_i
-2.073		0.013	0.259		0.159						-9.657	0.000
-2.326		0.019	0.289		0.157				0.000		-9.397	0.259
-2.936		0.027	0.314	-0.047	0.194				0.000		-8.682	0.975

-2.337		0.022	0.287		0.151	0.002			0.000		-8.311	1.346
-2.524		0.019	0.275	-0.037	0.188						-8.179	1.478
-1.669			0.177		0.153						-8.173	1.483
-2.520	0.007	0.029	0.285		0.129	0.003			0.000		-8.025	1.631
-1.499			0.206		0.150					-0.011	-7.973	1.683
-2.048		0.014	0.254		0.154	0.002					-7.745	1.911
-2.166	0.004	0.016	0.257		0.148						-7.719	1.938

I. Araneae. Adjusted R^2 of full model = 0.446.

Intercept	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature	AICc	Δ_i
-9.408					0.339	0.025	0.017			0.072	71.318	0.000
-7.999					0.323	0.019				0.045	71.584	0.266
-6.407					0.272	0.023					71.883	0.565
-6.194		-0.021			0.283	0.021					73.991	2.672

J. Gymnosperm. Adjusted R^2 of full model = 0.400.

Intercept	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature	AICc	Δ_i
0.008				0.150							62.649	0.000
12.208	-0.060	-0.227		0.162					-0.002	-0.186	62.839	0.190
13.501	-0.056	-0.209							-0.002	-0.210	63.050	0.400
-0.683			0.676	0.201							63.301	0.652
7.390		-0.151							-0.002	-0.182	63.375	0.725
3.783		-0.064								-0.103	63.490	0.840
2.153										-0.051	63.523	0.874
1.732											63.562	0.912
11.299	-0.054	-0.217	0.670	0.182					-0.002	-0.197	63.902	1.253

1.907								-0.001			63.906	1.257
5.826		-0.164		0.150					-0.002	-0.158	63.948	1.298
9.008	-0.051	-0.109								-0.122	63.971	1.322
2.232			0.726							-0.075	64.078	1.428
5.488		-0.159	0.771	0.174					-0.002	-0.174	64.146	1.497
15.017	-0.068	-0.226						-0.001	-0.002	-0.194	64.215	1.565
0.049		-0.034		0.202							64.295	1.646
2.135		-0.070		0.135						-0.076	64.595	1.946
14.623	-0.064	-0.217	0.762					-0.001	-0.002	-0.205	64.647	1.998
7.323		-0.145	0.640						-0.002	-0.199	64.656	2.006

Figure Legends

Figure 1. The independent (dark grey) and joint (light grey) contributions (given as R^2 values) of ten explanatory variables for the number of established alien species in each region for magnoliophyta (Mag), insects (Ins), nematodes (Nem), birds (Bir), chromista (Chr), fungi (Fun), myriapods (Myr), mammals (Mam), araneae (Ara) and gymnosperms (Gym), as estimated from hierarchical partitioning.

Figure 2. Scatterplots showing the relationships between globalisation index and number of established alien species for (a) magnoliophyta, (b) insects, (c) nematodes, (d) birds, (e) chromista, (f) fungi, (g) myriapoda, (h) mammals, (i) araneae and (j) gymnosperms. The effect of the strongest predictor in each taxon (area for gymnosperms and GDP for the rest) was controlled for by multiplying log-transformed area/GDP and the relevant coefficient given in the model with the smallest AICc (see Table 1) then subtracting from log-transformed number of alien species.

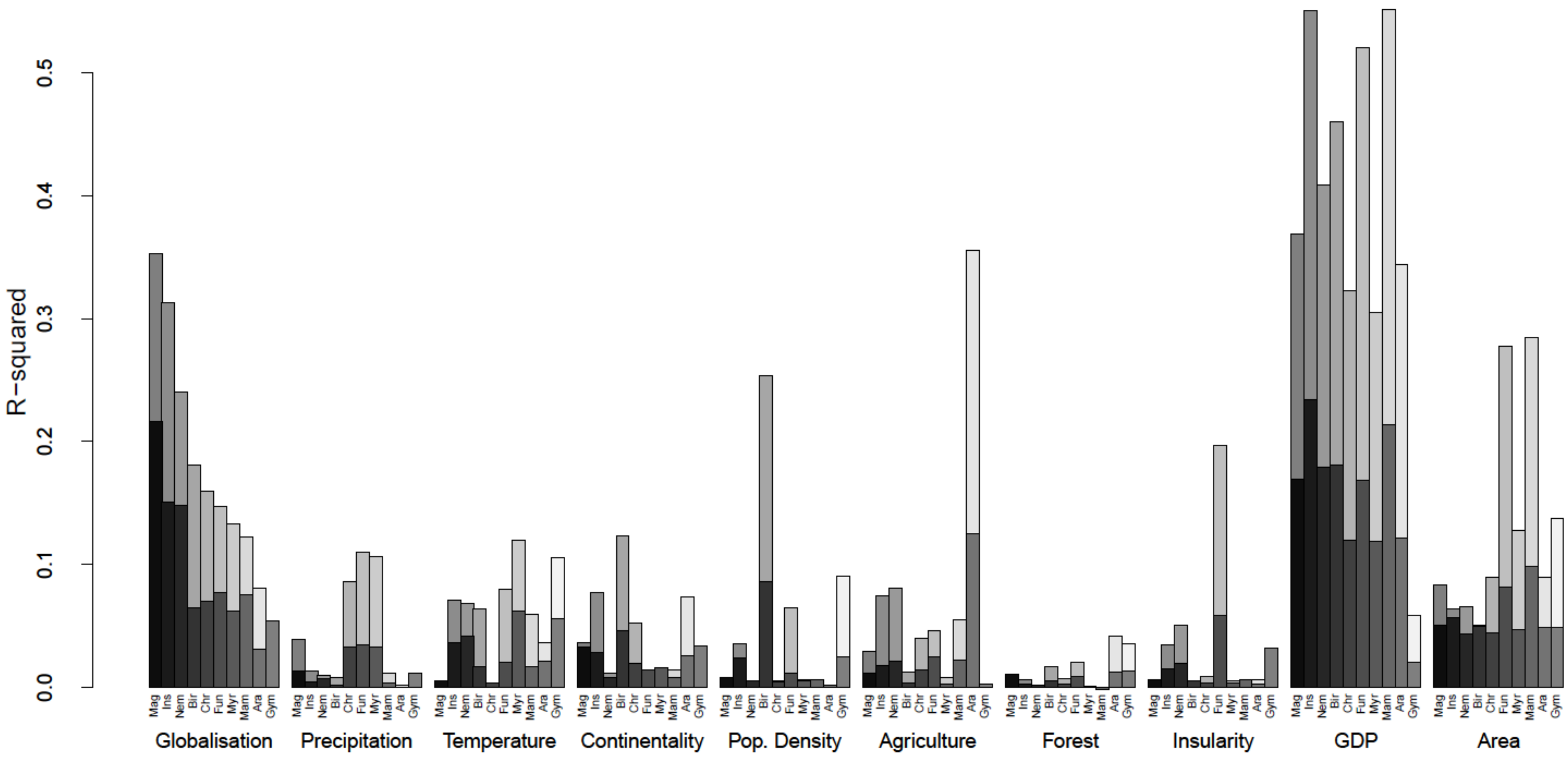
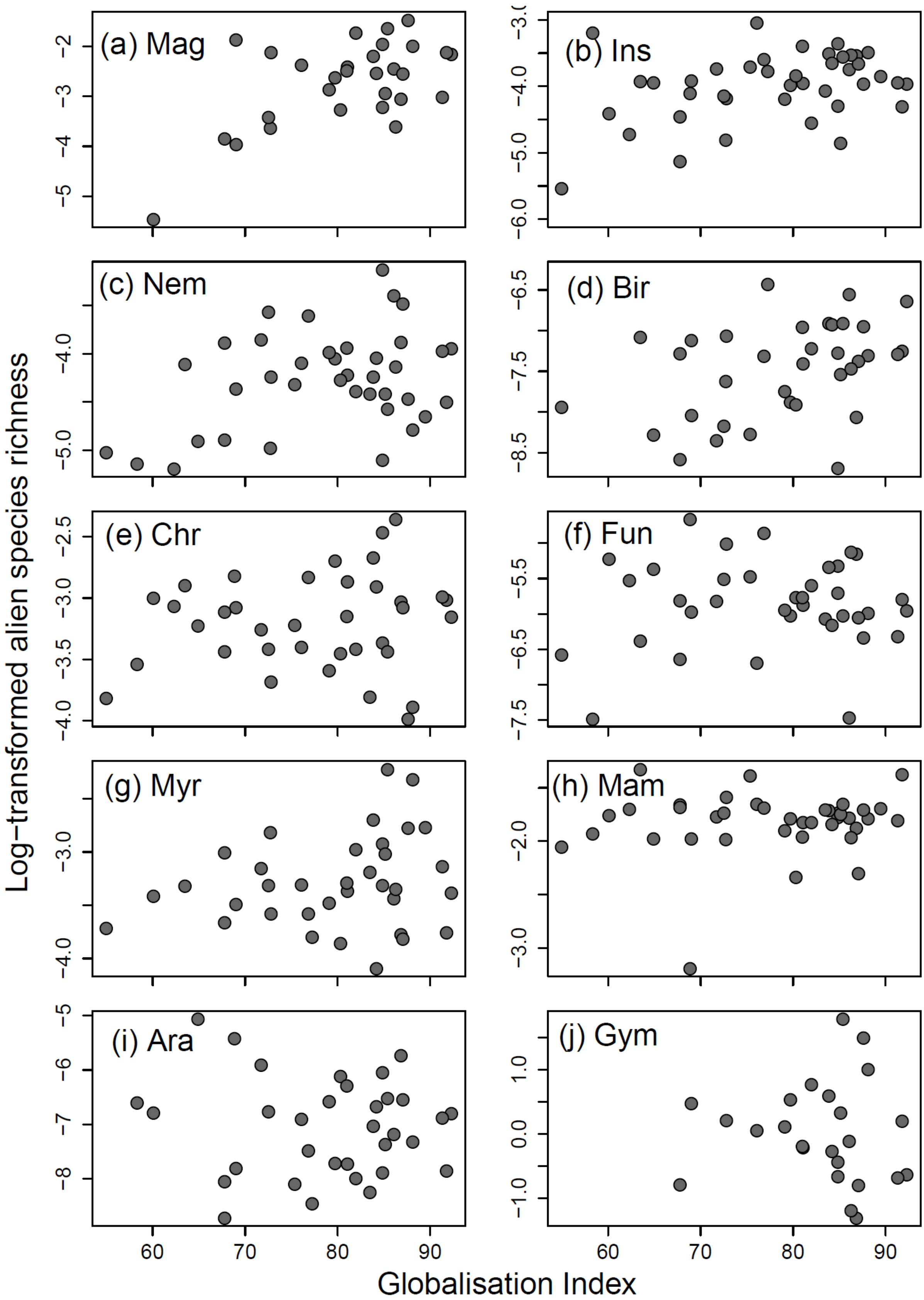

R−squared
0.0
0.1
0.2
0.3
0.4
0.5
Mag Ins Nem Bir Chr Fun Myr Mam Ara Gym
Globalisation
Precipitation
Temperature
Continentality
Pop. Density
Agriculture
Forest
Insularity
GDP
Area

Figure 1.



(a) Mag
(b) Ins
(c) Nem
(d) Bir
(e) Chr
(f) Fun
(g) Myr
(h) Mam
(i) Ara
(j) Gym
Log−transformed alien species richness
Globalisation Index
60
70
80
90

Figure 2.

Supplementary material

Table A1. Pearson product-moment correlation coefficients between potential explanatory variables. Correlations greater than 0.8 or less than -0.8 are highlighted in bold.

	Globalisation index	Continentality	Insularity	log (Area)	log (GDP)	% Agricultural land	% Forest	Population density	Annual precipitation	Annual temperature
Continentality	-0.469									
Insularity	0.065	-0.483								
log (Area)	-0.052	0.477	-0.031							
log (GDP)	0.426	0.229	-0.282	0.749						
% Agricultural land	-0.033	-0.114	-0.124	0.080	0.378					
% Forest	-0.063	0.512	-0.596	0.238	0.226	-0.171				
Population density	0.147	-0.175	-0.068	-0.602	-0.368	0.064	-0.408			
Annual precipitation	0.245	-0.358	-0.010	-0.247	-0.154	-0.086	-0.021	0.013		
Annual temperature	0.065	-0.530	-0.022	-0.442	-0.002	0.407	-0.191	0.213	-0.055	
Road density	0.601	-0.234	-0.071	**-0.819**	-0.427	0.145	-0.141	**0.991**	0.101	0.207

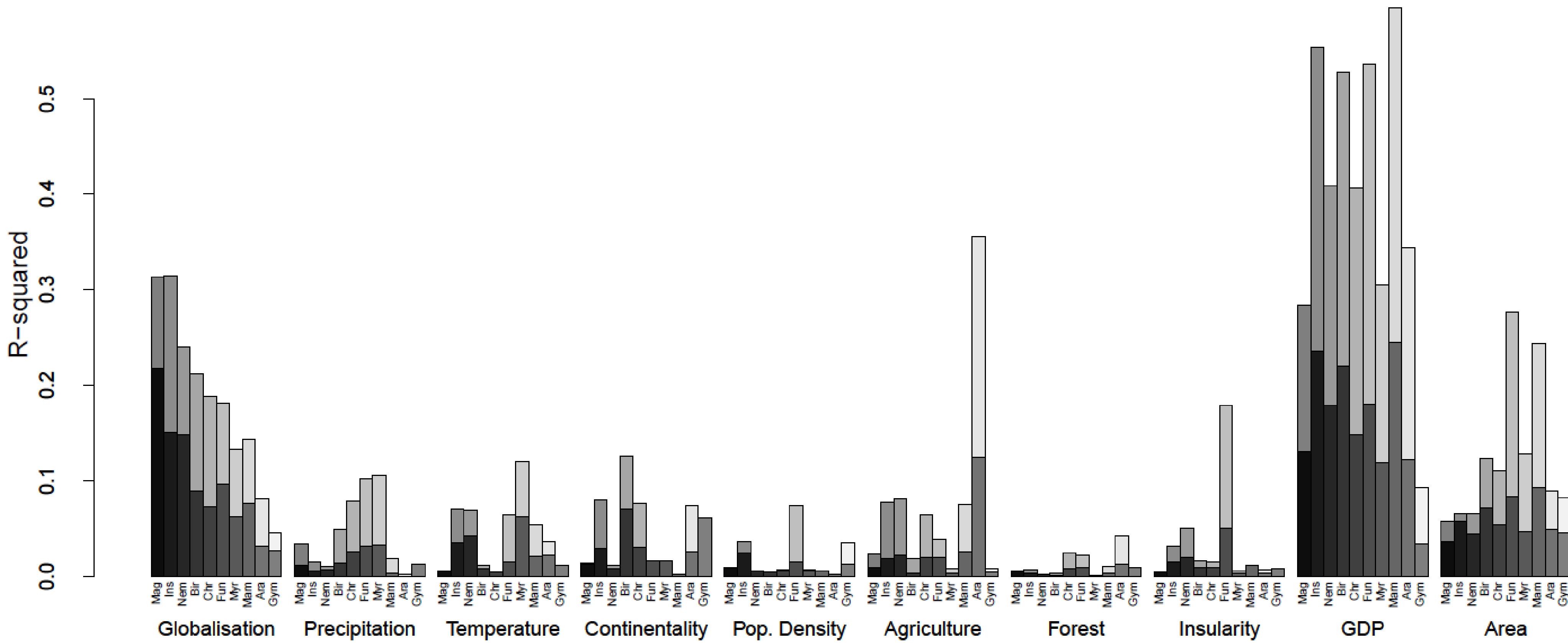


Figure A1. The independent (dark grey) and joint (light grey) contributions (given as R^2 values) of ten explanatory variables for the number of all introduced alien species in each region for magnoliophyta (Mag), insects (Ins), nematodes (Nem), birds (Bir), chromista (Chr), fungi (Fun), myriapods (Myr), mammals (Mam), araneae (Ara) and gymnosperms (Gym), as estimated from hierarchical partitioning.

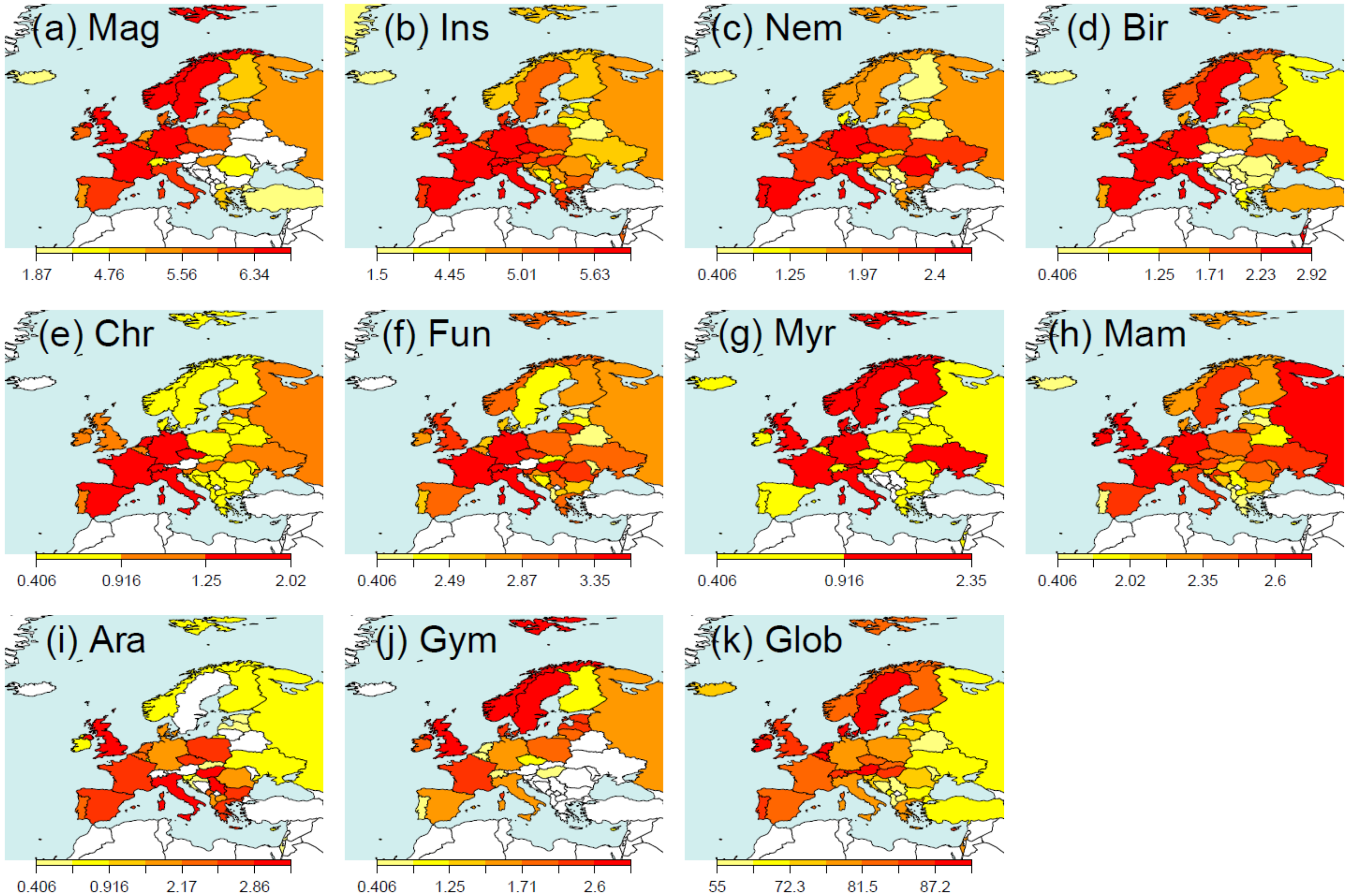


Figure A2. Maps showing spatial variation across Europe and the numbers of established alien species for each taxa: (a) magnoliophyta, (b) insects, (c) nematodes, (d) birds, (e) chromista, (f) fungi, (g) myriapoda, (h) mammals, (i) araneae, (j) gymnosperms and (k) the globalisation index. The numbers of alien species are log-transformed values.